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Habitat configuration affects spatial pattern of β diversity of insect communities breeding in oyster mushrooms

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Abstract. Theory predicts that spatial structure can mediate interactions that affect species diversity in a patchy environment. A rarely considered effect of spatial structure on biodiversity is the interplay of spatial habitat arrangement with species interactions at multiple spatial scales. We investigated how spatial habitat arrangement and predation mediate the assembly of the larval communities of fungivorous insects breeding in the oyster mushroom, *Pleurotus ostreatus* (Jacq. ex Fr.) P.Kumm in a North American woodland. In a two-way factorial design, we varied the spatial arrangement of mushroom clumps ('clustered', 'patchy', and 'uniform'; 3 levels) crossed with predator exclusion (access allowed or not; 2 levels) to study their joint effects on patterns of α , β and γ diversity of the fungivorous insect communities. Partitioning diversity into these three components suggested that neither spatial nor predation treatments significantly affected α , β and γ diversity. We found that an intermediate inter-clump distance (i.e., the 'patchy' treatment) increased spatial autocorrelation in insect community composition within experimental blocks, particularly in the mushrooms to which predators had access. The spatial structuring in β diversity indicates that the arrangement of mushroom clumps can structure β diversity of fungivorous larval communities through direct effects on the species themselves (e.g., increased aggregation and habitat choice of ovipositing females of fungivorous insects), as well as effects mediated through the presence and behavior of predators (e.g., spatially structured selective foraging by predators acting as a filter on which species were in the clumps). The naturally patchy nature of mushroom fruiting may transform the spatial pattern of β diversity by altering the behavior of ovipositing females, or by weakening the negative effect of larval competition.

Key words: aggregation; fungivore; habitat arrangement; *Pleurotus ostreatus*; predator-mediated coexistence; spatial autocorrelation; spatial heterogeneity.

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INTRODUCTION

One advance in community ecology over the last decade has been an increased recognition that spatial heterogeneity is key to maintaining biodiversity at multiple spatial scales. Spatial heterogeneity in the distributions of organisms arises for many reasons, including dispersal

limitation (Holyoak and Lawlor 1996, Kneitel and Miller 2003, Cadotte 2006), environmental heterogeneity (Worthen et al. 1994), history (Kadowaki et al. 2012), and interactions with other organisms (Chesson and Kuang 2008). One of the most studied features of spatial heterogeneity, both theoretically and empirically, is the isolation of habitats, which can affect dispersal

among habitats and thus local communities. Theoretical work on metacommunities suggests that intermediate isolation can maintain the greatest average local diversity, for example when immigration rescues inferior competitors or more susceptible prey from extinction (Shurin and Allen 2001, Mouquet and Loreau 2003). In contrast, a high level of movement among habitats can eliminate spatial refuges from competition and predation through regional homogenization (Shurin and Allen 2001, Mouquet and Loreau 2003). Empirical studies have shown that the distance between subdivided habitats, as a proxy for the degree of isolation and level of immigration, can have positive, negative or no effects on local diversity (Huffaker 1958, Kareiva 1987, Holyoak and Lawlor 1996; see Cadotte 2006 for review) depending on the connectivity among local habitats and the dominant biotic interactions (e.g., competition and predation) in a region.

In nature, habitats are often patchy and aggregated at several spatial scales (Inouye 2005). The variety of patterns present at multiple spatial scales cannot be fully encapsulated by the simple concept of isolation; the spatial arrangement of subdivided habitats could influence biodiversity in complex ways. The spatial arrangement of habitats could determine the outcome of competitive interactions through changing the distribution of individuals among habitats and thus the relative strength of intra- versus interspecific competition (Inouye 2005, Hart and Marshall 2009). Experiments using mushroom-breeding flies show that spatial aggregation of the fly larvae increased with increasing spacing among mushroom patches (Heard 1998, Takahashi 2006), with possible consequences for biotic interactions among them. While there have been several studies exploring how spatial habitat structure mediates species interactions that affect species diversity in a patchy environment (Huffaker 1958, Srivastava 2006, Spiesman 2012), a more complete understanding of the roles of spatial heterogeneity in natural systems on diversity will require investigation into the effects of spatial habitat arrangement at multiple spatial scales.

The concept of α , β , and γ diversity provides a useful tool to quantify diversity patterns at multiple spatial scales (Whittaker 1960), and the

partitioning of diversity may allow us to infer possible mechanisms underlying local community assembly (Anderson et al. 2011). In particular, β diversity accounts for variation or turnover in identities of species across localities, and links the diversity in individual localities (α diversity) to the total diversity in a larger area (γ diversity) (Anderson et al. 2011). Systems with high variation among local communities (hence high β diversity) indicate that either spatial processes (colonization-extinction dynamics) or environmental filtering and strong environmental gradients across localities contribute to the overall diversity in the area. In contrast, systems with low β diversity but high α diversity suggest that local processes maintain the overall diversity in the area (species sorting), or that colonization rates are so high that communities within local habitats are affected more by immigration than by interspecific interactions (mass effects, sensu Shmida and Ellner 1984). Patterns of α and β diversity could change with dispersal patterns, which do not necessarily have consequences for γ diversity (Mouquet and Loreau 2003).

Fungus-insect communities are a prime candidate model system with which to study the effects of spatial habitat arrangement on diversity (Worthen 1989a, Kadowaki et al. 2011). Mushrooms are a patchy food and habitat for a vast diversity of arthropods (Shorrocks et al. 1979, Jaenike and James 1991, Wertheim et al. 2000). Insects feeding on mushrooms (fungivorous insects) are mostly small-bodied habitat specialists. The assembly of a community of fungivorous insects upon mushroom clumps occurs via colonization by adults (the dispersal stage) followed by competitive interactions among the larvae. Because insect larvae generally cannot disperse among different clumps of mushrooms, individuals from multiple species in discrete mushroom clumps can be viewed as a set of interacting communities linked by dispersal, i.e., a metacommunity (Worthen et al. 1996). In addition, predators are widespread in fungal habitats, and can affect fungivore insect communities in important ways (Worthen 1989a, Worthen et al. 1994), with potential effects on prey diversity. For example, predators can moderate competition among fungivorous insects breeding in mushrooms of *Agaricus bisporus* (J. Lange) Imbach and facilitate coexistence among the

fungivorous insect community (Worthen 1989a).

We investigated how spatial habitat arrangement and predation mediate the assembly of larval communities of fungivorous insects breeding in the oyster mushroom, *Pleurotus ostreatus* (Jacq. ex Fr.) P.Kumm., in a North American woodland. We posit that the spatial arrangement of mushroom clumps can alter α and β diversity in the fungivorous insect communities. We make two specific predictions. First, increasing distance among clumps will decrease α diversity (species richness at the scale of a single mushroom clump) and increase β diversity (variation or turnover of species composition across mushroom clumps) and γ diversity (total number of species from a collection of mushroom clumps). This pattern could arise because insect species show stronger spatial aggregation with more isolated clumps (e.g., Heard 1998, Takahashi 2006), and increased larval aggregation drives extinction of species in some clumps but produces refuges from competition in others and thus favors increased β and γ diversity at the cost of α diversity (Heard and Remer 1997). On the other hand, aggregated clumps of mushrooms (i.e., narrower spacing among clumps) are more likely to be found by all species and could allow competitively superior species to outcompete inferior competitors, thus lowering both α and β diversities (i.e., very short distances between clumps will reduce the role of any competition-colonization trade-off, if one exists). Second, we hypothesize that the presence of predators and spatial arrangement of mushroom clumps can interact in their effects on both α and β diversity of the fungivorous larval community. For example, predators may reduce the negative effect of larval competition on α diversity if predators preferentially remove competitively superior species (i.e., predator-mediated coexistence; Holt and Hoopes 2005). When predators adopt different foraging strategies according to the spatial arrangement of mushroom clumps, their selective foraging on a particular set of mushroom clumps could influence distributions of the fungivorous larval community.

METHODS

Study area

Our 150 m \times 80 m experimental site was in a secondary oak-pine forest in Elinor Klapp-Phipps

Park, Tallahassee, Florida, USA (30°31'54" N, 84°18'00" W). The forest canopy was primarily composed of *Quercus virginiana* Mill (Fagaceae), *Pinus taeda* L., *P. glabra* Walter (Pinaceae) and *Liquidambar styraciflua* L. (Altingiaceae). Vines (e.g., *Smilax bona-nox* L., *Vitis rotundifolia* Michx.) and herbs (*Cayratia* sp., *Toxicodendron radicans* (L.) Kuntze) dominated the ground cover (Appendix: Fig. A1A).

Study organisms

The oyster mushroom, *Pleurotus ostreatus*, forms tight clumps of fruiting bodies on dead and living deciduous trees in spring and autumn. The pale mushroom cap is 4–14 cm diameter, and the white stalk that supports it is 1.5–2.0 cm (Appendix: Fig. A1B). Oyster mushrooms occur naturally in the park, but were not found in the study site during the study period. Insects that feed on oyster mushrooms include generalist fungivores (Drosophilidae, etc.), specialist fungivores (Erotylidae, etc.; Cline and Leschen 2005), detritivores or scavengers (Sphaeroceridae, etc.). We focused on the community of insect larvae, which are restricted to mushroom clumps and are potentially strong competitors, and did not attempt to characterize transient mobile adult insects. Ground-crawling predators are widespread in fungal habitats, including ants (Formicidae: Hymenoptera), earwigs (Dermaptera), rove beetles (Staphylinidae: Coleoptera) and ground beetles (Carabidae: Coleoptera).

Experimental design

We employed a two-way factorial design, including three spatial arrangements (clustered, 'patchy', and uniform distributions of mushroom clumps; Fig. 1A–C), and two levels of predator treatment (access by ground-crawling predators allowed or not), replicated three times over 18 experimental spatial blocks (10 m \times 10 m). Each spatial block contained a set of seven mushroom clumps (Fig. 1A–C). The locations of spatial blocks were randomized in the study area to create variation in nearest neighbor distances (Fig. 1D). Clumps of fresh oyster mushrooms were randomly assigned to treatment blocks. Each clump of mushroom (mean = 54.7 g, range = 42.8–68.8 g) was placed in clear plastic rectangular container (ca. 600 cm³) containing 200 g of ant-free potting soil at the bottom, and

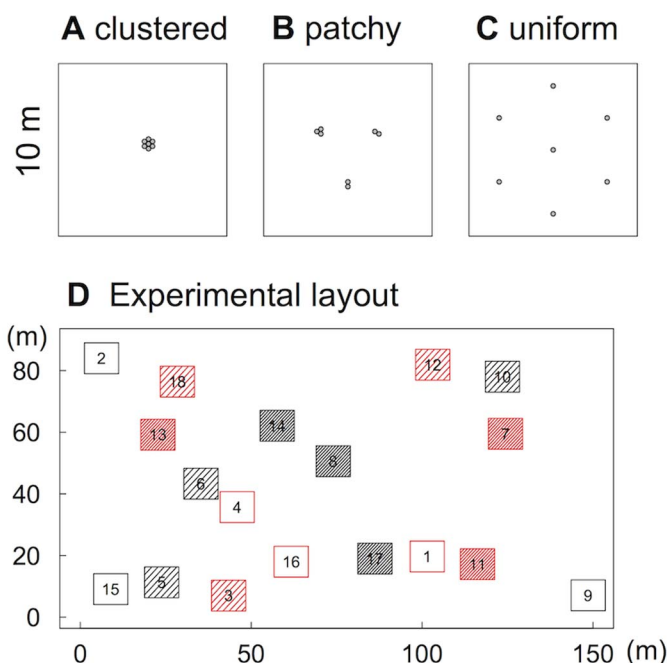


Fig. 1. Spatial arrangement of mushroom containers (or clumps) (A–C) and experiment layout (D): (A) clustered treatment (dense hatching squares), (B) patchy treatment (light hatching squares) and (C) uniform treatment (open squares). Average inter-clump distances were 0.41 m (clustered), 2.91 m (patchy) and 5.41 m (uniform). (D) A total of 18 spatial blocks (10 m × 10 m) were placed randomly in the study site (150 m × 80 m) to create variation in the nearest neighbor distances between individual blocks. Three spatial and two predator access treatments were assigned to blocks in a complete randomized design. Red squares had ants excluded; black allowed ant access.

represented the local scale in which competition and predation among insects occur. Large access holes were cut in all four sides of each mushroom container to allow insects to colonize the mushrooms. We applied Tanglefoot adhesive (Con-tech, Canada) below the holes for the predator exclusion treatments. For treatment with predator access, four vertical bands of tangle-trap were applied to the corners: this allowed potential predators to enter the cup while controlling for attractant or repellent properties of the Tangle-foot.

A total of 126 mushroom containers (or clumps) were available for insects to colonize for one week (1–7 May 2011) (Appendix: Fig. A1C). During the colonization period, mushrooms were moistened with water-spray (25.0 ml per cup) to prevent desiccation. When containers were collected, we counted trapped individuals of beetles and flies to check whether Tanglefoot influenced their colonization (Lewis and Worth-

en 1992, Worthen et al. 1994). All the mushrooms were then transferred into new incubation cups (600 cm³) with 250 g of potting soil. Our predator exclusion was effective, but did not necessarily exclude flying predators. Instead, winged predators (e.g., Staphylinidae: *Borboropora quadriceps* (LeConte) and hymenopteran parasitoids (adult Braconidae)) were removed before transferring to new incubation cups.

The incubation cups were kept in ambient conditions in the laboratory over three weeks (Appendix: Fig. A1D). Mushrooms were moistened every two or three days, and emerged adults were collected, identified to genus or morphospecies, and counted. We collected 44 insect species, 27 of which were considered to be fungivorous.

Statistical analysis

All analyses were conducted using R v. 2.15 (R Core Team 2013) with the package ‘vegan’

(Oksanen et al. 2013) and the graphics package 'lattice' (Sarkar 2008). We quantified treatment differences in species richness of the fungivore insect communities at the scale of mushroom container (α diversity) and spatial block (γ diversity), and differences in species composition across mushroom containers (β diversity) at the end of the incubation period.

Alpha diversity was averaged by spatial blocks and analyzed using spatial and predation treatments as predictors in the framework of ANOVA and general linear model. γ diversity was analyzed using generalized linear models with a Poisson distribution and log link ('glm' function). Treatment differences in species composition at the block scale were tested using PERMANOVA (Anderson 2001; 'adonis' function in the package 'vegan'). We quantified differences in species composition using the Raup-Crick dissimilarity index (Chase et al. 2011; 'raupcrick' function in 'vegan') that allows us to quantify the turnover of species identities independent of changes in species richness; it ranges from -1 to $+1$, indicating whether insect communities are more (approaching $+1$) or less (approaching -1) dissimilar than expected by chance.

We tested for two aspects of β diversity, (1) average pairwise community dissimilarity, and (2) spatial autocorrelation of species composition within block. First, for individual spatial blocks, we calculated pairwise community dissimilarity (Raup-Crick dissimilarity index) for all 7 mushroom containers, using analysis of multivariate homogeneity of group dispersions (variances) (PERMDISP, Anderson 2006; 'betadisper' function in 'vegan'). The average pairwise community dissimilarity (β diversity) was analyzed as a function of the spatial and predation treatments in the framework of ANOVA.

Second, we analyzed the spatial structure of β diversity within spatial blocks. We calculated Mantel spatial autocorrelation statistics for individual blocks (Fig. 1D), using two distance matrices, one matrix describing pairwise β diversity among mushroom containers within the block and the other describing Euclidean distances among the mushroom containers (Fig. 1A–C). P values for Mantel correlation statistics were obtained from 9999 permutations of the matrices. The Mantel correlation coefficients were analyzed as a function of the spatial and

predation treatments using general linear model.

RESULTS

Of 44 insect morphospecies (hereafter species) collected, approximately two thirds were obligate fungivores or detritivores. For statistical analysis, we included all these species ($N = 27$) except non-fungivore species.

Spatial arrangement of the mushroom clumps had no significant effect on local species richness (α diversity) at the scale of mushroom container ($F_{2,12} = 1.911$, $P = 0.190$). There was no significant effect of predator exclusion on α diversity ($F_{1,12} = 1.253$, $P = 0.285$) (Fig. 2A). In predator exclusion treatments, α diversity was 23 % and 35% higher in the 'patchy' treatment compared to the clustered ($t = -0.731$, $P = 0.479$) and uniform treatments ($t = -1.737$, $P = 0.108$), respectively.

There were no block level difference in species richness (γ diversity) among the spatial treatments ($F_{2,12} = 1.278$, $P = 0.314$) and predation treatments ($F_{1,12} = 0.009$, $P = 0.927$) (Fig. 2B). There was no significant interaction between the treatment combinations ($F_{2,12} = 1.522$, $P = 0.258$). In predator exclusion treatments, γ diversity was 27 % and 30% higher in the 'patchy' treatment compared to the clustered ($z = -1.100$, $P = 0.271$) and uniform treatments ($z = -0.716$, $P = 0.474$), respectively. PERMANOVA could not detect any significant effects of spatial arrangement and predation treatments on species composition at the block level (Table 1).

In the analysis of β diversity, there were no significant differences in average pairwise β diversity among spatial and predator access treatments (Table 2A, Fig. 3A). We found that the 'patchy' treatments were marginally more likely to have greater average β diversity compared to the clustered treatment ($t = -1.822$, $P = 0.093$). An interaction term between the 'patchy' and predator exclusion treatments was also marginally significant ($t = 1.890$, $P = 0.083$). For the spatial autocorrelation in β diversity (Table 2B), the 'patchy' treatment had the highest correlation between turnover in identities of insect species and inter-clump distances within block, remarkably in the containers to which predators had access, i.e., there was an interactive effect of spatial and predation treatments on spatial structure in β diversity (Fig. 3B). While

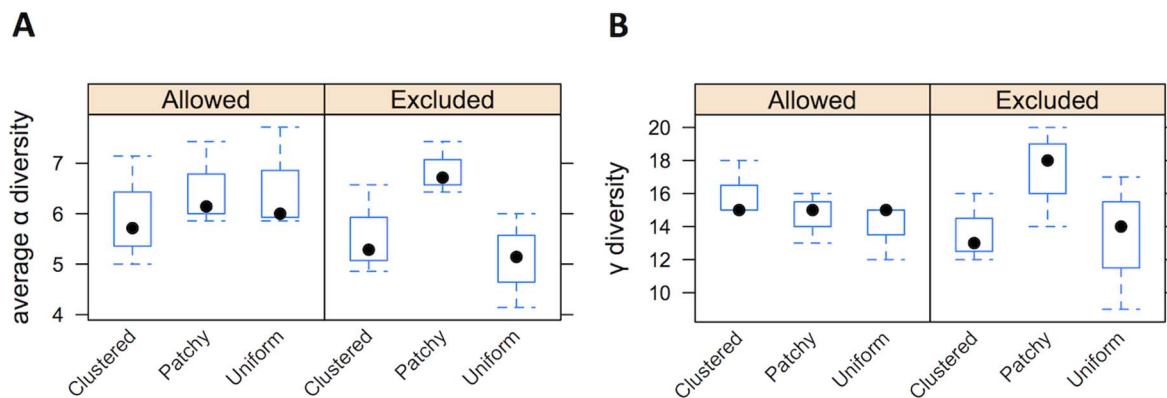


Fig. 2. Effects of spatial arrangement and predator access treatments on α diversity (the scale of mushroom container) and γ diversity (the scale of experimental spatial block), in units of species richness of the insect larval communities in oyster mushrooms.

there were positive Mantel correlation coefficients for ‘patchy’ \times predator access communities in two of the three blocks (Appendix: Table A1), we found at most very weak spatial autocorrelation for the other treatment combinations (Appendix: Table A1). For the ‘patchy’ treatment, seven mushroom containers were arranged among three sets (Fig. 1B), and individual sets of containers were occupied by different insect species within blocks. Thus, spatial arrangement and predator exclusion interacted in their effects on spatial structure of β diversity. It should also be noted, however, that some of the patterns presented in this study are barely significant (for example, Table 2B), and should not be considered very robust given the study-wise error rate generated by a dozen statistical tests.

DISCUSSION

A growing body of literature suggests that spatial heterogeneity, over a wide range of spatial

scales, supports biodiversity in nature (e.g., Worthen et al. 1994, Inouye 2005). Our experimental study was set up to address the potential effects of spatial habitat arrangement, costs of colonization movements, ability to detect mushrooms, and how those patterns in effective colonization may interact with local competition and predation. Our results show that changing the small-scale spatial arrangement of mushroom clumps (local habitats) did not affect average α , β , or γ diversity, but the spatial structuring of β diversity was greatest in the ‘patchy’ treatments to which predators had access. Thus, while there was no significant main effect of predation on the average level of β diversity itself, predator exclusion interacted with spatial arrangement in its effect on the spatial structuring of the insect community. This indicates that, notwithstanding at most very weak effects on diversity patterns, our treatments effectively affected the fungivorous insect species themselves, as well as mediated the impacts of their predators. The lack of a stronger

Table 1. Permutational multivariate analysis of variance (PERMANOVA) testing for the effects of spatial arrangement of mushroom containers (or clumps) and predator access on fungivorous insect community structure at the experimental spatial block scale (γ diversity).

Variable	df	F	R ²	P
Spatial arrangement	2	0.491	0.060	0.823
Predation	1	0.840	0.051	0.538
Spatial arrangement \times predation	2	1.251	0.153	0.298
Residuals	12		0.735	
Total	17		1.000	

Table 2. Results of general linear models testing for treatment effects on (A) average β diversity within experimental block, and on (B) spatial structure of β diversity i.e., Mantel spatial autocorrelation coefficient within spatial blocks ($N = 18$). The clustered treatment and predator non-exclusion treatment are the baseline for other comparisons.

Variable	Coefficient	SE	<i>t</i>	<i>P</i>
(A) Average β diversity				
Intercept	0.426	0.032	13.109	0.000
Patchy (vs. Clustered)	−0.034	0.046	−0.734	0.477
Uniform (vs. Clustered)	−0.084	0.046	−1.822	0.093
Predator excluded (vs. allowed)	−0.042	0.046	−0.907	0.382
Patchy \times Predator excluded	0.123	0.065	1.890	0.083
Uniform \times Predator excluded	0.086	0.065	1.318	0.212
(B) Spatial structure of β diversity (Mantel spatial autocorrelation)				
Intercept	−0.052	0.117	−0.448	0.662
Patchy (vs. Clustered)	0.498	0.166	3.007	0.011
Uniform (vs. Clustered)	0.079	0.166	0.479	0.641
Predator excluded (vs. allowed)	0.204	0.166	1.230	0.242
Patchy \times Predator excluded	−0.623	0.234	−2.661	0.021
Uniform \times Predator excluded	−0.147	0.234	−0.626	0.543

effect of the predator treatment may be due in part to dry weather during the 1-week colonization period. Ants can have stronger negative effects on larval survivorship in moist habitats than in dry habitats (Worthen et al. 1994).

Studies of insects exploiting ephemeral resources (mushrooms, rotten fruits, dung, etc.) have demonstrated that spatial aggregative responses are a key mechanism regulating their diversity in the patchy environment (e.g., Atkinson and Shorrocks 1984, Wertheim et al. 2000,

Inouye 2005, Takahashi 2006, Kadowaki 2010, Fader and Juliano 2013). Theory predicts that when resource clumps are sparsely distributed (entailing high travel costs), it would be adaptive for females to produce fewer, larger clutches because they have fewer chances to encounter resource clumps (Heard and Remer 1997). One could therefore expect that varying the average isolation distance from less (our ‘clustered’ treatment) to more isolated (our ‘uniform’ treatment) could increase larval aggregation at

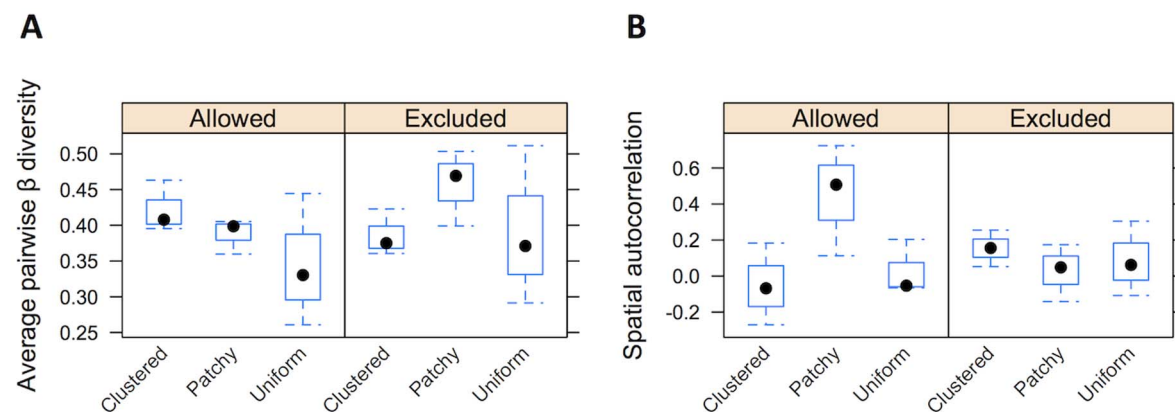


Fig. 3. Effects of spatial arrangement and predator access treatments on two different aspects of β diversity: (A) average pairwise dissimilarity and (B) spatial autocorrelation in community dissimilarity. (A) For individual spatial blocks ($N = 18$), average community dissimilarity to centroid was calculated using the Raup-Crick dissimilarity index, and analyzed as a function of spatial arrangement and predation treatments. (B) The Mantel spatial autocorrelation coefficient (spatial structure of β diversity) of the insect communities in mushroom containers within spatial blocks. High Mantel r values indicate that distant mushroom containers consist of more distinct communities, i.e., community similarity decays rapidly with distance within block.

the scale of mushroom clumps, thereby driving extinction of inferior competitors in some clumps and producing refuges from competition in others (i.e., increased β diversity at the cost of α diversity). In the present study, we were unable to find any strong signal of either decreased α diversity or increased β diversity when resource clumps are sparsely distributed. It is important to note, however, that there were relatively strong effects on diversity that were not close to statistical significance (e.g., Fig. 2 and Table 2), indicating that the statistical power in our study was probably low and we therefore suggest that the jury is still out.

Our results revealed the greatest spatial structuring in β diversity at an intermediate inter-clump distance (patchy treatment; Fig. 3B); there was significant spatial autocorrelation within two of the three blocks of the patchy \times predator access treatments (Appendix: Table A1), whereas there was no spatial autocorrelation for the other treatment combinations. What are the underlying mechanisms behind this spatial structuring of β diversity? We propose spatial autocorrelation in this patchy \times predator access treatment and the lack thereof for other spatial treatments could arise from three non-mutually exclusive possible mechanisms: (1) increased aggregation of ovipositing females and/or increased clutch size laid by females (Heard and Remer 1997, Heard 1998, Takahashi 2006), (2) predators' selective foraging on a particular set of mushroom clumps, or (3) habitat choice by ovipositing females responding differently to the presence of predators. We minimized the effects of habitat heterogeneity (and hence habitat filtering) on diversity through using approximately the same weight of fresh mushrooms (clump) in each container, thus it is likely that the strongest spatial structuring in β diversity occurred either through altering the behavior of ovipositing females, or through weakening the negative effect of larval competition. One caveat to inferences about patterns of oviposition is that we did not directly examine egg or larval abundances; that would require thorough dissections of the mushrooms, or adding extra resources during rearing to relax interspecific competition and density-dependent mortality (Jaenike and James 1991).

A next step towards better understanding the

maintenance of diversity in ephemeral mushrooms is to extend the timescales of study. Although insects in ephemeral patches are not likely to be at an equilibrium state, or at least not at the scale that we used for the analysis, the turnover of individual mushrooms produced by the same mycelium may create resource clumps that persist for longer periods (Worthen and McGuire 1990), with concomitant effects of the colonization of prey fungivores and their predators. The membership in the communities hosted by individual mushroom clumps could be influenced by localized community development over time, because fungivorous flies can recruit over time to areas richer in mushrooms (Worthen 1989b). In more applied contexts, it is a key challenge to know if changes in spatial patterns and the phenology of mushroom fruiting (induced by environmental change or anthropogenic factors; Kausrud et al. 2008) can alter the diversity patterns of fungivorous insects at large spatial scales or over longer time-scales.

CONCLUSIONS

Our study shows that the naturally patchy nature of mushroom fruiting may control spatial structuring of β diversity of insect communities, either by affecting the behavior of ovipositing females, or by weakening the negative effects of larval competition. Although the results show that neither spatial nor predation treatments significantly affected α , β and γ diversity, there were relatively strong effects on diversity that were not close to statistical significance, possibly due to low replication and statistical power. Our work has implications for metacommunity ecology by illustrating how more realistic metacommunity descriptions can include spatial arrangements of local habitats and connectivity. Combining the use of graph-theory (Urban and Keitt 2001) with concepts from metacommunity ecology could lead us to more explicitly evaluate the full effects of spatial habitat configuration on the dynamics of species interactions in a spatially heterogeneous landscape.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Treatment effects on spatial autocorrelation (a key aspect of β diversity) of the insect communities in mushroom clumps within experimental blocks. To test for interclump-distance dependent changes in insect community dissimilarity within blocks, the Mantel r statistics were calculated using distance matrices accounting for compositional turnover of β diversity separate from changes in α diversity (Raup-Crick dissimilarity index) and Euclidean distance among pairs of mushroom clumps. See Fig.1 for the locations of plots in the study area.

Block	Spatial arrangement	Predator	Mantel r	P
1	Uniform	Excluded	-0.106	0.724
2	Uniform	Allowed	0.201	0.195
3	Patchy	Excluded	0.169	0.218
4	Uniform	Excluded	0.057	0.428
5	Patchy	Allowed	0.108	0.283
6	Patchy	Allowed	0.724	0.005
7	Clustered	Excluded	0.045	0.45
8	Clustered	Allowed	-0.27	0.859
9	Uniform	Allowed	-0.058	0.621
10	Patchy	Allowed	0.505	0.003
11	Clustered	Excluded	0.156	0.273
12	Patchy	Excluded	0.049	0.381
13	Clustered	Excluded	0.253	0.131
14	Clustered	Allowed	0.176	0.216
15	Uniform	Allowed	-0.062	0.680
16	Uniform	Excluded	0.301	0.068
17	Clustered	Allowed	-0.064	0.591
18	Patchy	Excluded	-0.139	0.744

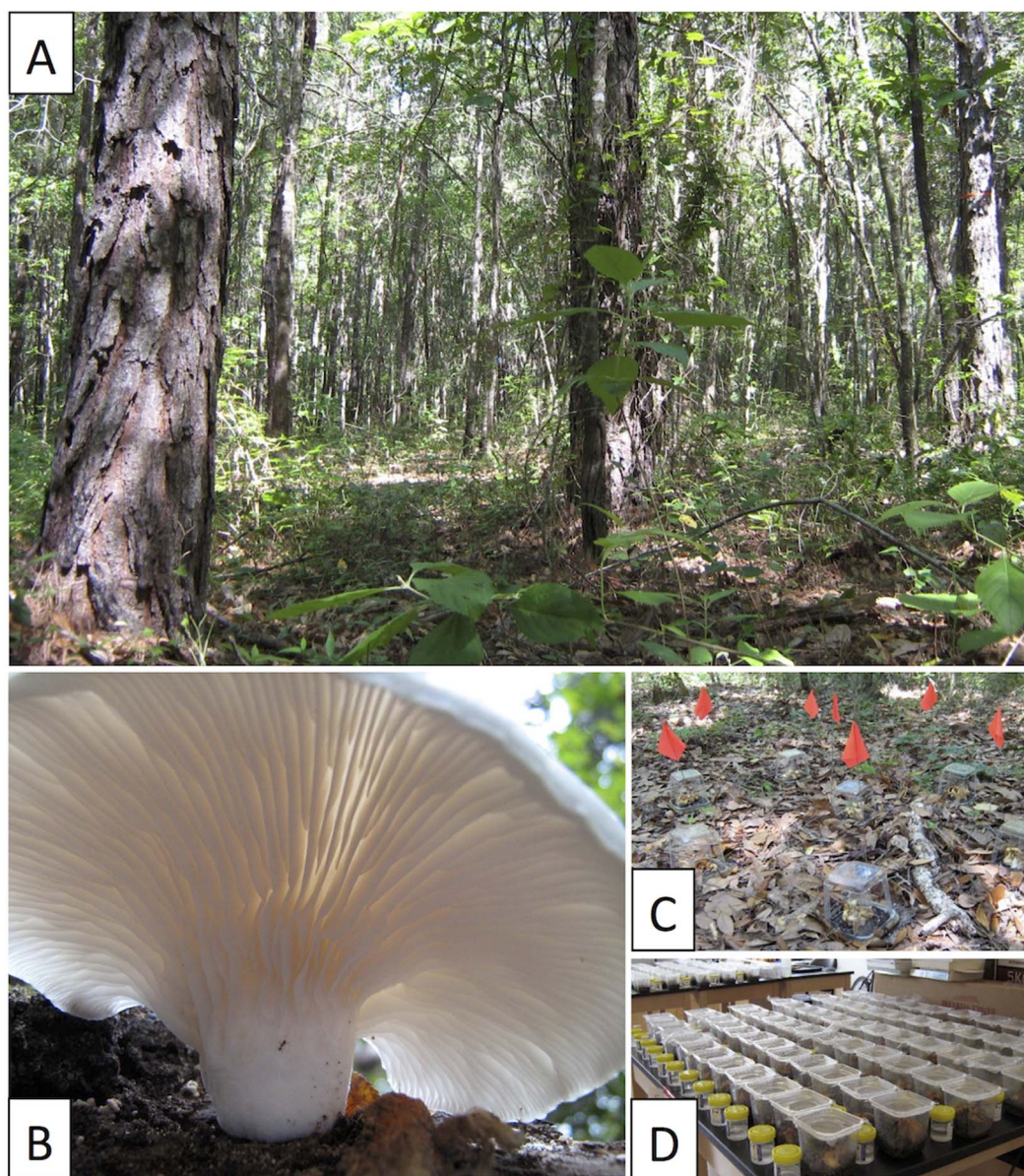


Fig. A1. Study organism and its habitat. (A) The forest floor of the study site in Elinor Klapp-Phipps Park, Tallahassee, Florida. (B) Fresh, natural fruitbody of the oyster mushroom, *Pleurotus ostreatus*, which was found outside the study area. (C) Mushroom clumps (in plastic containers) were available for insects to colonize in the study site. (D) Incubation cups used for rearing.